

A multispecies test of source-sink indicators to prioritize habitat for declining populations

Julie A. Heinrichs^{1,3*}, Joshua J. Lawler¹, Nathan H. Schumaker², Chad B. Wilsey¹, Kira Newcomb^{1,3}, Cameron L. Aldridge³

¹School of Environmental and Forest Sciences, University of Washington, P.O. Box 352100, Seattle, WA 98195-2100, U.S.A

²Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, 97331, U.S.A

³Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523-1499, U.S.A

*Julie.Heinrichs@colostate.edu (Corresponding Author)

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Abstract:

For species at risk of decline or extinction in source-sink systems, sources are an obvious target for habitat protection actions. However, the way in which source habitats are identified and prioritized can reduce the effectiveness of conservation actions. Although sources and sinks are conceptually defined using both demographic and movement criteria, simplifications are often required in systems with limited data. To assess the conservation outcomes of alternative source metrics and resulting prioritizations, we simulated population dynamics and extinction risk for three endangered species. Using empirically-based habitat-population models, we linked habitat maps with measured site or habitat-specific demographic conditions, movement abilities, and behaviors. We calculated source-sink metrics over a range of time periods of data collection and prioritized the strongest sources for conservation. We then tested the ability of prioritized patches to identify the most habitats most affecting persistence by removing them and measuring the population response. Our results indicated that conservation decisions based on different source-sink metrics and durations of data collection can impact species persistence. Shorter times series obscured the ability of metrics to identify influential habitats, particularly in temporally variable and slowly declining populations. Data-rich source-sink metrics that included both demography and movement information did not always identify the habitats with the greatest influence on extinction risk. In some declining populations, patch abundance better predicted influential habitats for short-term regional persistence. As source-sink metrics (i.e., births-deaths; births and immigrations – deaths and emigration) describe net population conditions and cancel out gross population counts, they may not adequately identify influential habitats in declining populations. For many non-equilibrium populations, new metrics that maintain the counts of

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individual births, deaths, and movement may provide additional insight into habitats that most influence persistence.

Introduction

Many species at risk of decline or extinction are suspected to operate in source-sink systems, wherein some areas are net exporters of individuals, and others are net importers (Pulliam 1988). In source-sink systems, sources are an obvious target for habitat protection (Margules & Pressey 2000; Carroll et al. 2003); however, it is seldom possible to conserve all source habitats and habitat prioritization of is often required. Identifying local populations as sources (Howe et al. 1991) or sinks can be an important first step in prioritizing habitats (Runge et al. 2006). Prioritizing strong sources can further direct habitat conservation decisions through identifying consistent, high-output sources, rather than sinks or areas that fluctuate among sources and sinks (Heinrichs et al. 2016). However, the methods by which sources and sinks are identified greatly differs among studies (Furrer & Pasinelli 2016), driven by the constraints of data collection and availability. With the use of many methods to quantify source-sink dynamics, we know little about the effectiveness of alternative approaches to identifying key habitats that influence long-term persistence.

Defining sources and sinks is a data-intensive task, requiring an understanding of the demographic and movement characteristics of each discrete population or habitat. Theoretical metrics generally define sources as areas where births outweigh the number of deaths and where births and immigrations outweigh deaths and emigrations (Holt 1985; Pulliam 1988). However, empirical methods of identifying sources and sinks often fall short of conceptual formulations due to challenges in demographic and movement data collection (Peery et al. 2006; Furrer & Pasinelli 2016). Simple metrics are used in place of more data-intensive conceptualizations, including site-specific counts of terrestrial animals (i.e., abundance; Gilroy & Edwards 2017), local population growth rates, or a combination of abundance and inter-population movement rates etc. (Furrer & Pasinelli 2016). These measures are prone to misclassifications of sources and sinks as they do not account for underlying demographic and movement mechanisms that result in differential population conditions (Runge et al. 2006; Gilroy & Edwards 2017). As simple source-sink metrics could result in the continued protection of sinks, some have cautioned against their use for prioritizing habitats for species conservation (e.g., Hanski 1998).

More complex source-sink metrics use mark-recapture data to estimate survival and fecundity and evaluate sources and sinks by virtue of the balance of births and deaths (e.g., Breininger & Oddy 2004; Walker et al. 2016). Others additionally evaluate patch contributions based on demographic and emigration information (Runge et al. 2006), or link together multiple lines of inference (e.g., abundance, demography, movement exchanges, genetic conditions) to assess source-sink status (e.g., Caudill 2003; Andreasen et al. 2012; Contasti et al. 2013). As more types of data are used to define local population and habitat conditions, greater confidence is often awarded to source-sink assessments and their ability to identify source habitats that greatly influence population persistence (hereafter referred to as influential habitats). However, this assumption is largely untested.

Species at risk of decline and extinction are often in need of immediate action, and decisions on which population and habitats to protect are limited by available data and the resources to enact protection on the ground. Important conservation decisions are made on as little as a few years of data, and considered robust if informed by 5-10 years of data. When

few years of data are available, we often expect data-rich metrics (e.g., complex source-sink metrics) to better identify influential local habitats and populations than data-poor metrics (e.g., patch abundance), particularly if source-sink dynamics are temporally stable (Howe et al. 1991; Watkinson & Sutherland 1995; Gilroy & Edwards 2017). Yet stochastic or cyclic variation can obscure the long-term contributions of habitats to population persistence within short time-frames (Runge et al. 2006; Contasti et al. 2013), leading to sub-optimal habitat prioritizations and conservation outcomes. In particular, sources that behave like sinks when densities are high (i.e., pseudo-sinks) can exhibit high temporal variability (Watkinson & Sutherland 1995; Dias 1996; Johnson 2004). If sources are assessed only during times of low population density, rather than across a spectrum of population densities, their contributions to persistence could be overestimated.

To examine the degree to which different prioritization approaches are able to identify the most influential habitats impacting long-term regional population persistence, we simulated population dynamics and habitat prioritization outcomes for three endangered species: Black-capped vireos (*Vireo atricapilla* in Texas), Greater Sage-grouse (*Centrocercus urophasianus* in Alberta), and the Ord's kangaroo rat (*Dipodomys ordii* in Alberta). Using empirically-parameterized habitat-population models, we linked habitat maps with measured site-specific or habitat type-specific demographic conditions, movement abilities, and behaviors. We calculated a range of source-sink metrics to create alternative habitat prioritizations. We re-sampled long-term simulated data to create short-term data series and re-calculated the source-sink metrics. We then tested the ability of each metric prioritizations (for each time period) to identify the most influential habitats by removing them from the system and simulating the population response. Those with the greatest response (i.e., increase in extinction risk) best characterized the most influential patches for long-term persistence.

Using this approach, we expected the most biologically detailed metrics and longer time series to identify the habitats with the greatest contributions to persistence. As the combination of demographic and movement information allows the disentanglement of gains via reproduction versus immigration (and losses via death versus emigration), we expected demography- and movement-informed metrics (i.e., BIDE) to best identify the most valuable habitats (e.g., Figueira & Crowder 2010). We expected demography-only and abundance metrics to be weaker in their ability to identify sources and influential habitats, particularly using short time series. In highly dynamic systems (i.e., those with high variation in intra- or inter-annual demography and population densities), we expected longer time series of data would be required to evaluate and prioritize populations (Gonzalez & Holt 2002; Loreau et al. 2013). We expected that the choice of metric and the duration of data collection would matter most for species with slow or moderate rates of decline, where subtle differences among local populations can accumulate over time to greater extent than in rapidly declining species. Lastly, we expected high-abundance sinks to be important landscape elements that could outweigh the influence of some source habitats. In declining populations where a large proportion of the population occupies sink patches, the removal of high abundance patches could result in a large reduction in population size (Howe et al. 1991; Heinrichs et al. 2015). If extinction risk is more responsive to removals that limit population size than those targeting the most productive sources, abundance may better indicate the most influential habitats for short-term persistence.

Methods

Case Studies

We simulated movement, habitat selection, demography, and emergent source-sink dynamics for three endangered species: Black-capped Vireos at Fort Hood, Texas (U.S.A), Ord's kangaroo rats, and Greater Sage-grouse in Alberta, Canada. These species represent a range of small and declining populations, landscape conditions, population variability, and ecological contexts in which source contributions to population persistence may differ. Populations differed in their rates of decline, degrees of stochastic variability, and strength of source-sink dynamics, and were subject to different drivers of source-sink dynamics (e.g., parasitism, low-quality habitat).

We used previously developed spatially explicit individual-based models and baseline predictions for our case study species: The Ord's kangaroo rat (Heinrichs et al. 2010), Black-capped vireo (Wilsey et al. 2013), and Greater Sage-grouse (Heinrichs et al. 2017). All models made extensive use of empirical habitat and population data and were constructed in the HexSim simulation modeling environment (Schumaker et al. 2017). Habitat conditions (habitat availability, structure, habitat selection values, habitat quality etc.) were linked to population outcomes based on previously parameterized relationships of individual interactions with the landscape for each species. Through this process, sources and sinks were emergent properties arising from individual movement and habitat selection decisions identified by empirically modeled species-habitat maps, and the parameterized demographic consequences of residing in their chosen location(s).

Slower decline in a small population

In southeastern Alberta, the Ord's kangaroo rat (hereafter kangaroo rat), occupies discrete sandy habitat patches, including actively eroding sand dunes or blowouts, partially-stabilized sand dunes, and the margins of sandy roads (Gummer et al. 1997; Gummer 1999; COSEWIC 2006). Differential habitat quality among habitat types gives rise to source-sink dynamics (Heinrichs et al. 2010, 2015). Source, high quality habitat includes actively eroding and natural sandy areas where overwinter survival and predation risk is lower. Conversely, low quality sink areas include disturbed sandy areas and sandy road margins that are associated with higher predation and parasitism risk, lower forage quality, colder burrow temperatures, and lower over-winter survival rates (Teucher 2007). The population experiences substantial intra- and inter-annual population fluctuations in abundance (COSEWIC 2006), with high reproductive rates leading to the opportunistic occupancy of low quality habitats within a year, and variable overwinter survival causing inter-annual fluctuations (Kenny 1989; Gummer et al. 1997; Gummer & Robertson 2003). We used the baseline scenario developed by Heinrichs et al. (2010), in which we simulated realistic scenarios of kangaroo rat population dynamics, with sources, sinks, and pseudo-sinks emerging as a result of differences in habitat quality among habitat types, and high inter-annual variation in survival. This system represented the slowest rate of population decline and most gradual increase in extinction risk among the case study systems (Fig. 1).

Rapid decline in a larger population

The Fort Hood military installation hosts more than >5000 male Black-capped Vireos (Cimprich & Heimbuch 2012; Wilsey et al. 2013), occupying relatively discrete shrub habitat patches along with Brown-headed Cowbirds (*Molothrus ater*). Cowbirds often parasitize vireo nests, particularly in low quality habitat (created by military training activities) creating ecological traps (Remes 2000) that limit vireo persistence in the absence of cowbird control (Battin 2004; Wilsey et al. 2013). In baseline simulations, the number and strength of source habitats depended on the prevalence of nest-parasitism (Heinrichs et al. 2015). In alternative

scenarios, we simulated realistic scenarios of vireo population dynamics both in the presence and absence of cowbird control (developed by Wilsey et al. 2013) and assessed source-sink dynamics under both alternatives (Heinrichs et al. 2015). In the absence of cowbird control, vireos were subject to high nest parasitism rates (75% in high- and 85% in low-quality habitat; Wilkins et al. 2006). Under cowbird control, vireos were subject to low nest parasitism rates (5% in high- and 15% in low-quality habitat). The high parasitism scenario represented the scenario with the most rapid decline from the largest initial population size (Fig. 1). Environmental stochasticity was represented in fecundity, adult, and juvenile survival rates by annually drawing from representative distributions (see Wilsey et al. 2013), and resulted in a lesser degree of population variation than kangaroo rats. Sources could become pseudo-sinks with changes in local population densities. To assess the influence of population trend on modeling outcomes, we compared this rapidly declining high parasitism scenario with the stable low parasitism scenario.

Decline in a smaller population

In Alberta, the critically endangered Greater sage-grouse occupies a fragmented sagebrush landscape in southeastern Alberta, moving seasonally among nesting, summer, and winter resource areas (Aldridge & Boyce 2007; Carpenter et al. 2010). As a sagebrush obligate species, habitat use is constrained by the availability of sagebrush cover, and site selection is guided by fidelities to breeding, natal, nesting locations, and avoidance of development (Aldridge & Boyce 2007). Baseline simulations indicated that sources were embedded among sinks throughout the sage-grouse range in Alberta, and evident in areas with high nest success and chick survival (Heinrichs et al. 2017). Conversely, sinks emerged in high-selection habitats with reduced chick survival and/or nesting success (Aldridge and Boyce 2007, Heinrichs et al. 2017). We used the baseline scenario developed by Heinrichs et al. (2017) to represent a very small population with an intermediate rate of decline (Fig. 1). Stochastic variation was represented in survival and reproduction by annually drawing from representative distributions (see Heinrichs et al. 2017). This induced variable population densities through time, but at a lesser magnitude than those observed for kangaroo rats.

Simulations

We linked empirical habitat selection models that were developed for each species to empirically-derived population data, including population sizes, demographic rates, densities, range sizes, movement, and behavior data. Within the spatially explicit individual-based models, simulated individuals dispersed among habitat areas to select a range with suitable resources or conditions. The quality of the range influenced population density, survival, and/or reproductive rates. For kangaroo rats, habitat type-specific survival rates described variation in habitat quality. The sage-grouse model used demographic risk maps to specify locations with higher and lower likelihoods of nest success and chick survival. In vireo scenarios, habitat suitability values were used to indicate areas of low and high quality habitat, associated with higher and lower nest parasitism (see Appendix S1). All models included pre-emptive density-dependent habitat selection, wherein areas with the best resources relative to local competition were chosen and occupied. Models also included varying magnitudes of environmental stochasticity, corresponding to the estimated variation in empirical survival and/or reproduction rates. The details of each model, including model

starting conditions, are in Heinrichs et al. (2010), Wilsey et al. (2013), Heinrichs et al. (2017), Heinrichs et al. (2015), and outlined in the Supporting Information (Appendix S1).

The source-sink status of a patch was determined by the collective experiences of individuals within a given habitat. Patch occupancy and abundance was influenced by patch size, quality, location, landscape context, shape, resources, and local conditions. Further, the source-sink status of a patch was influenced by species and population attributes including life history characteristics, location-specific demographic rates, population densities, movement abilities, and site fidelities. For kangaroo rats and vireos, discrete (contiguous) patches were used as the spatial unit of source-sink evaluation. For sage-grouse, we used hexagonal pixels to summarize data on population size, births, deaths, immigrations, and emigrations (See Appendix S1).

To classify sources and sinks and assess source strength, we used three different metrics, ranging in complexity and data requirements. 1) Productivity: The total number of births minus deaths was recorded for each patch. Patches in which the number of births exceeded deaths over the simulation time period were deemed sources (and vice versa for sinks). 2) BIDE: Movement was explicitly counted in BIDE as (births + immigration) – (death + emigration) for a given patch. 3) Abundance: Lastly, we calculated the mean number of individuals occupying each patch at the end of the year. For each species, we sorted and ranked patches based on their metric values. Strong ‘sources’ were indicated by large positive values and prioritized for conservation. In each system, we selected a small proportion of sources to test the ability of metrics to reliably identify a small number of patches with the strongest influences on persistence. Prioritizations resulted in prioritizing 25 and 50 kangaroo rat patches, 12 and 23 vireo patches, and 10 and 20 sage-grouse patches, using the same proportions of sources (0.39 and 0.78%) in each landscape. These arbitrary proportions were chosen to result in a number of patches for which habitat conservation actions could easily reasonably implemented. To evaluate the sensitivity of results to the proportion value, we explored two alternative proportions. Specifically, we expected to see greater differences in experiment outcomes when more patches were prioritized, resulting from the differing abilities of metrics to characterize the strengths of weaker sources.

We used the metrics calculated for the full duration of the baseline simulations (i.e., 35 years of data for sage-grouse, and 100 years for kangaroo rats and vireos years; 100 replicates) to represent a data-rich or the optimal information for each case study. To characterize how shorter time series of data collection could alter source-sink metric values and habitat prioritizations, we sub-sampled the baseline datasets and re-calculated all metrics using only 2, 5, and 10 years of data (using subset data for each species starting at time step 1 and using 100 replicates). To quantify the importance of priority patches for long-term persistence, we simulated the regional population outcomes of removing priority patches as indicated by all (3) metrics, calculated over all (4) time periods, and (2) source proportion scenarios. Source habitats were removed from habitat map(s) by replacing them with non-habitat matrix. Hence, simulated individuals could only use non-target sources, including the remaining weaker sources and all sinks. The probability of extinction (0 remaining

individuals; PE) was quantified through time (35 years for sage-grouse, 100 years for kangaroo rats and vireos). Simulation repetitions (25) were chosen to omit outliers while maintaining reasonable processing time. A quasi-extinction (QE) threshold of 1000 was used in place of PE for the low parasitism vireo scenario, as the population was stable. We plotted species-specific PE and QE results for each metric*time period combination to compare the performance of each metric in identifying the most influential source habitats. Metrics that resulted in higher PE predictions, based on the removal of source habitats, identified habitats that had greater influence on long-term persistence. Conversely, metrics associated with lower PE predictions were less effective at identifying influential sources, as their removal impacted the population to a lesser degree.

Results

Slower decline in a small, dynamic population

With the removal of key sources, the small kangaroo rat population declined to near-certain extinction within 45-90 time steps (Fig. 2). Over 100 years of simulated data collection, extinction risk (PE) was most sensitive to the removal of sources based on patch abundance, followed by productivity, and BIDE. As the period of data collection was reduced to 20 years or less, metrics made increasingly dissimilar predictions. When data collection was reduced to 5-10 years, the removal of key sources as predicted by the BIDE metric resulted in substantially lower risks of extinction than other metrics. At 2 years, source removals based on abundance resulted in the greatest extinction risk (indicating the most discernment in selecting influential habitats), then productivity and BIDE. Abundance generally yielded the best predictions and was the most robust to temporal data limitations. BIDE performed poorly in most time periods, worsening with fewer years of data collection. Productivity prioritizations were particularly sensitive to short (i.e., 2-5 year) time series of data. When fewer sources were prioritized and tested with removal (i.e., 25 instead of 50), extinction risks were more alike but the metrics rankings were similar (results not shown).

Rapid decline in a larger population

In the very rapid decline of vireos from the highest starting population size (under the high parasitism scenario), the removal of key habitats resulted in extinction in as little as 30 time steps, with a sharp threshold increase in extinction risk around 35 time steps (Fig. 3). Results were more similar among metrics through time compared to kangaroo rats, as the population rapidly trended towards extinction. Yet prioritizations still resulted in large differences in extinction risk within time steps 30-40. For example, around time step 35, productivity and BIDE resulted in a PE of ~ 0.25 versus ~ 0.70 for abundance. The greatest difference among metric results was observed with the longest time series. Among time periods, prioritizations based on abundance were the most effective at identifying influential habitats and productivity was generally the least discerning. As the data collection period was reduced, metric predictions became more similar.

Stable, large population - Black-capped vireo under low parasitism

When cowbird nest parasitism was controlled, the stable population did not result in extinction and had a low risk of falling to a quasi-extinction threshold of 1000 males (Fig. 4).

Prioritization metrics consistently identified similar habitat patches that hosted a large number of birds, deflating the long-term population size. Resulting risks of quasi-extinction were similar among all prioritization metrics and time periods.

Intermediate decline in a smaller population

The removal of key sources from the moderately sized sage-grouse population caused the risk of extinction to rapidly increase between 10 and 20 time steps (representing the years 2010-2020; Fig. 5). Differences among metric predictions were roughly similar for a given year. In the longest time series (35 years), extinction risk was most sensitive to habitats removed based on productivity. With only a few years of data collected, metrics informed by 2 years of data yielded somewhat opposite results. Productivity poorly identified influential habitats, and BIDE best predicted the most influential patches. There was little spread among other metrics, particularly with 5 and 10 years of data collection.

Discussion

Our results indicate that the methods by which habitats are conserved could impact species management outcomes. Yet, the importance of the choice of metric depends on the nuances of the ecological system including the rate of population decline and variability, the timing considered, duration of data collection, and the number of patches that are being prioritized. Simple metrics such as abundance outperformed more complex metrics at identifying key habitats that allow for persistence in some case studies, whereas complex metrics more accurately identified influential source habitats in others.

Simple metrics – Patch abundance

When source-sink dynamics are observed or suspected, management prioritizations often weigh protecting habitats with the largest number of animals against prioritizing putative sources. Simply prioritizing habitats based on abundance alone risks the misidentification of strong sinks, potentially compromising conservation outcomes (Hanski 1998). For example, abundance was a poor indicator of sage-grouse sources, with a 65-100% misclassification rate. Sage-grouse abundance was also ineffective at indicating influential habitats for regional persistence, particularly where grouse actively selected and flocked together in strong sink habitats with low nest success and chick survival (Aldridge & Boyce 2007).

By contrast, conserving high abundance sinks can actually be crucial for short-term viability of other species (Howe et al. 1991; Heinrichs et al. 2015). For example, abundance generally identified the most influential habitats for the short-term persistence of the black-capped vireo under high parasitism pressure. A very large number of vireos (~4000) occupied the targeted high abundance patches, all of which were sinks (using productivity and BIDE metrics, at all time periods). In comparison, minimal losses resulted from the removal of sources, indicating that smaller capacity sources were less influential than larger capacity sinks in avoiding near-term extinction (also see Howe et al. 1991; Heinrichs et al. 2015).

Complex metrics – Source-sink equations

For sage-grouse, metrics that included demography better identified influential habitats than abundance. Beyond the differences in population size and rate of decline among case

studies, the importance of including demography (i.e., productivity metric) and movement (BIDE) was also influenced by: 1) prioritization comparisons with limited variation in patch abundance because all patches were the same size, and 2) demographic risk maps that provided fine-scale spatial variation in demographic outcomes. Although BIDE outperformed simpler metrics when only a few years of data were collected, productivity resulted in equivalent conservation outcomes with longer data sets. This suggests that long-term evaluations (using 10 years of data or more) may not gain additional insight with the collection of movement data (See Appendix S1).

Contrary to expectations (e.g., Runge et al. 2006), BIDE was not always the best predictor of influential habitats, even in more slowly declining populations. In the variable kangaroo rat system, BIDE required more than 20 years of data to better identify influential sources than simpler metrics. BIDE also made underwhelming predictions for the rapidly declining vireo population. This resulted in part because: 1) extinction risk can be more responsive to low population sizes than to the presence of strong, productive sources, 2) BIDE's difference equation does not explicitly characterize the local population size, and thereby, does not fully convey magnitude of a declining population's impact.

BIDE is calculated based on the difference between factors that cause the population to grow (births and immigration) and shrink (death and emigration) and calculates the balance among these factors. As the counts of each event are effectively lost, a large but balanced population can have a BIDE value of 0, and small unbalanced populations can have very large BIDE values. Further, by subtracting emigrants, the BIDE equation can also undervalue small but highly productive sources that emit a large number of offspring that disperse elsewhere and support the declining population (e.g., small number of kangaroo rats in sand dunes). Net conditions and difference equations conveniently describe stable-state populations (Pulliam 1988); however, declining, non-equilibrium populations are not always regulated by density-dependent emigration and habitat selection (Caughley 1994), as assumed by traditional source-sink theory (Delibes et al. 2001). Hence, we suggest that source-sink calculations based on difference equations may not always be appropriate for identifying influential habitats for declining populations. Habitat prioritization decisions for declining populations likely need to weigh both abundance and source-sink strength in identifying the most influential patches to conserve, rather than inferring importance based on the net source-sink conditions.

Habitat Prioritizations for Effective Conservation

The means by which habitats are prioritized for declining species in source-sink systems may matter most for species with gradual rates of decline, dynamic population fluctuations, and those inhabiting large proportions of sink habitat (i.e., where abundance is a misleading indicator of source-sink status; Van Horne 1983). Simulated kangaroo rat populations persisted longer than vireo (high parasitism) and sage-grouse case studies, allowing this population more time to respond to habitat conditions than species with stronger declining trends. In more rapidly declining populations, the choice of metric still mattered, albeit over a shorter time frame (e.g., ~ 10 -15 years for sage-grouse and highly parasitized vireos). Large differences were observed among metrics within a given year, particularly for vireos

under high parasitism pressure, indicating that the loss of key habitats can have dramatic short-term consequences, and that conservation efforts that focus on improving high abundance sinks could be immediately helpful in increasing persistence (Vandermeer et al. 2010). In removing key sources and testing the result on extinction risk, we evaluated how remaining habitat could compensate for the loss of influential sources. Metrics that identified irreplaceable habitats resulted in greater impacts on extinction risks, indicating the contribution of these habitats to long-term persistence. Our analyses did not test the sufficiency of key habitats to support long-term persistence. However, future research could remove all but the key habitats and evaluate resulting extinction risk. In general, empirical experiments that test the ability of source-sink metrics to identify influential habitats (e.g., microcosms) for persistence through removal experiments could increase confidence in our model-based evaluations of source-sink metrics. Population metrics that additionally calculate a patch's location relative to the regional network may also be helpful in constructing simplified source-sink metrics.

Our results indicate that in source-sink systems, metrics identifying the most influential patches may need to simultaneously weigh patch abundance and source-sink contributions to persistence. Tailored metrics and new theory may be required to protect key habitats for declining species in source-sink systems and understand the conditions under which data collection can be simplified. Our three different case studies represented a range of population conditions, rates of decline, life histories and habitat selection behaviors; however, these do not represent all species and habitat conditions. To understand the ecological contexts in which new and existing source-sink metrics can indicate habitats that improve persistence, future analyses should explore a broader range of declining populations in source-sink systems.

Our results suggest that the choice and success of metrics may depend on a population's rate of decline, the degree to which temporal variability creates pseudo-sinks, and the proportion of the population occupying sink patches. Yet species differ broadly in how they select and compete for habitat and the degree to which they modify habitat through intensive use (Loehle 2012, 2013). Our species used contest competition to secure resources, and remained at or returned to familiar habitats where resources were not permanently altered. Future analyses should explore the sensitivity of source-sink metrics to alternative competition and habitat selection mechanisms (e.g., scramble competition), seasonal group movements, resource depletion (i.e., two-way interactions among population and habitat conditions), and directional habitat modification. Together, the complexities of non-equilibrium populations with diverse life histories and non-stationary environments may require a re-envisioning of tools, metrics and practical theory to identify the metrics and conditions under which metrics can be reliably used to indicate habitats that benefit population persistence.

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Figure Legends

Fig., 1. Log change in abundance and extinction risk (PE) in baseline scenarios (i.e., with all habitat), averaged over 100 simulation replicates. Ord's kangaroo rat female population size and PE were calculated for 100 time steps (beyond an initial 10-year burn-in time required for the model to approach the empirical population size; data not shown). Black-capped vireo male abundance and PE were calculated for the same (10-110) time steps in both cowbird control (vireo low) and no cowbird control (vireo high) in scenarios. Greater Sage-grouse male and female abundance and PE were calculated for time steps 1-35.

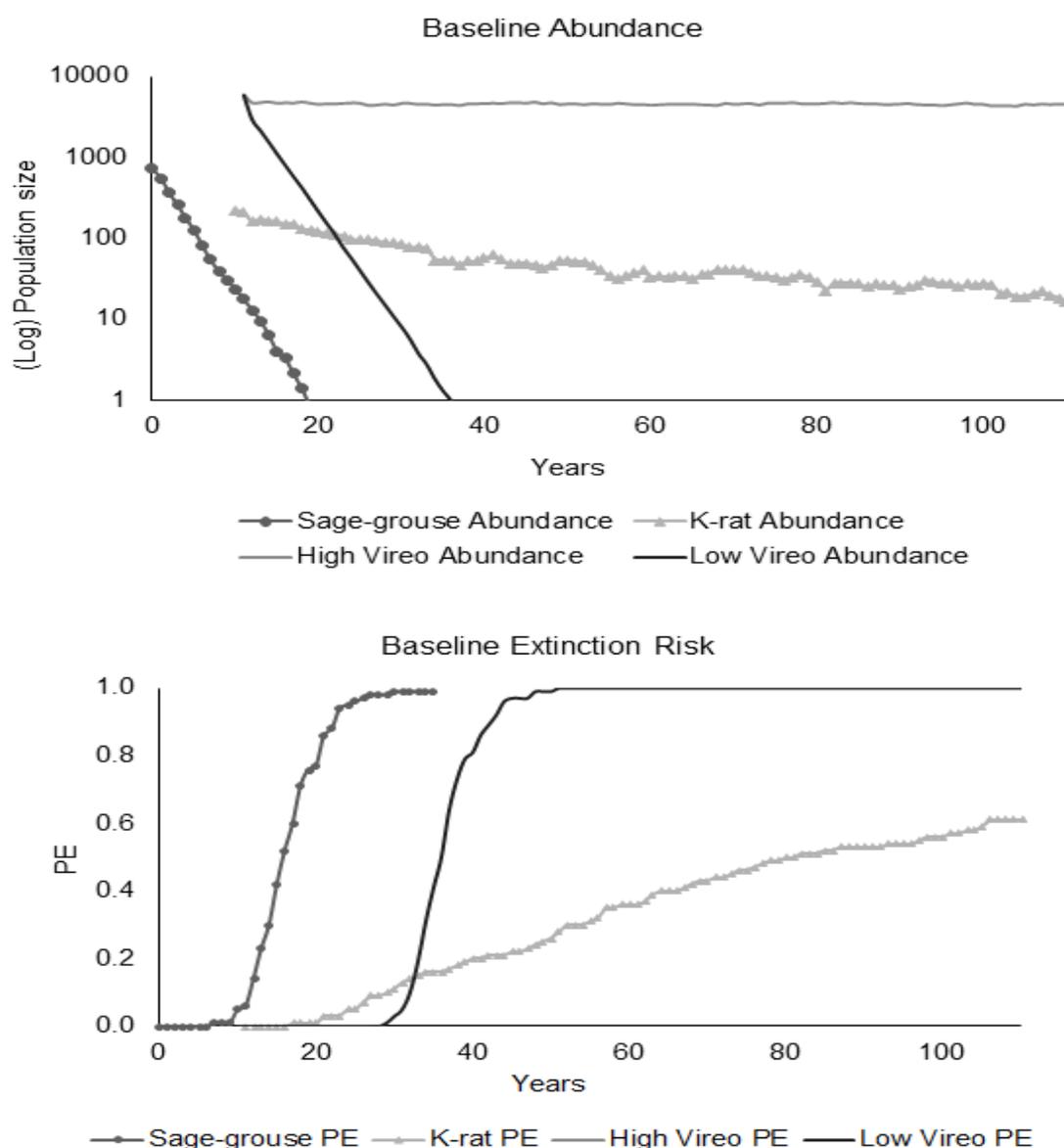


Figure 2. Ord's kangaroo rat (Alberta) extinction responses to key source habitat removals based on productivity, BIDE, and abundance-based source-sink metric prioritizations, calculated over 25 repetitions beyond the 10-year burn-in period. For a given year, higher Probability of Extinction (PE) values indicated metrics with greater predictive value in identifying habitats with greater importance to regional population outcomes.

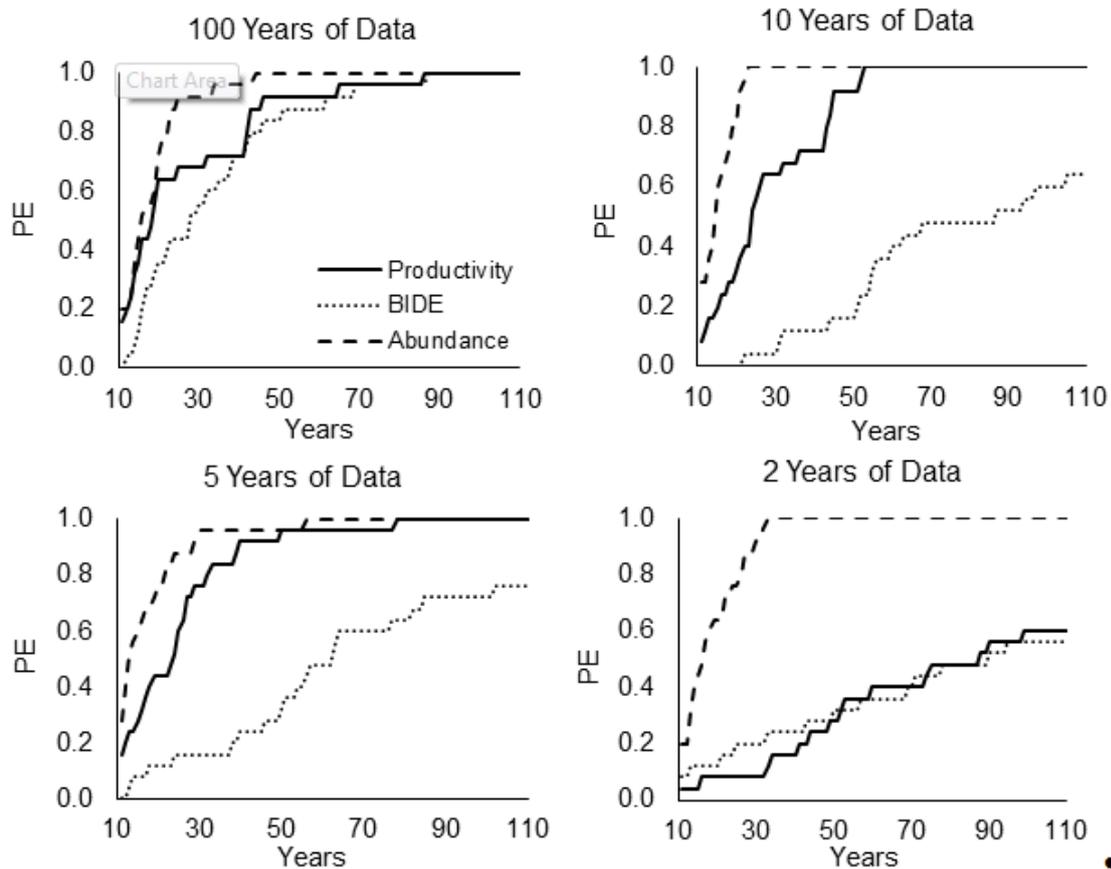


Fig. 3. Black-capped vireo (Texas) - high parasitism scenario extinction responses to key source habitat removals based on productivity, BIDE, and abundance-based source-sink metric prioritizations, calculated over 25 repetitions beyond the 10-year burn-in period (graphs truncated to years 25-55). For a given year, higher Probability of Extinction (PE) values indicated metrics with greater predictive value in identifying habitats with greater importance to regional population outcomes.

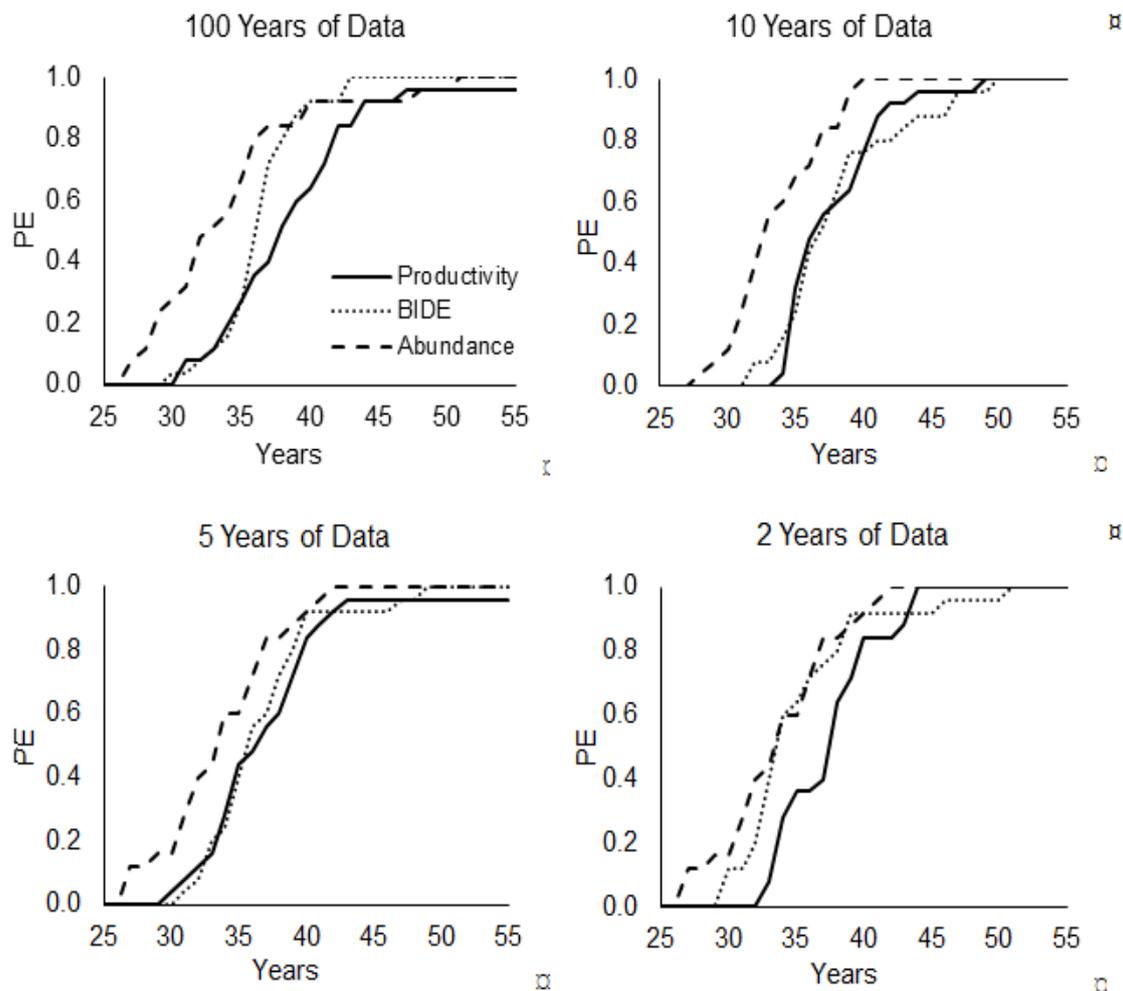


Fig. 4. Black-capped vireo (Texas) - low parasitism scenario extinction responses to key source removals based on productivity, BIDE, and abundance-based source-sink metric prioritizations, calculated over 25 repetitions beyond the 10-year burn-in period. For a given year, higher Quasi-Extinction probabilities (i.e., $QE < 1000$ males) indicated metrics with greater predictive value in identifying habitats with greater importance to regional population outcomes.

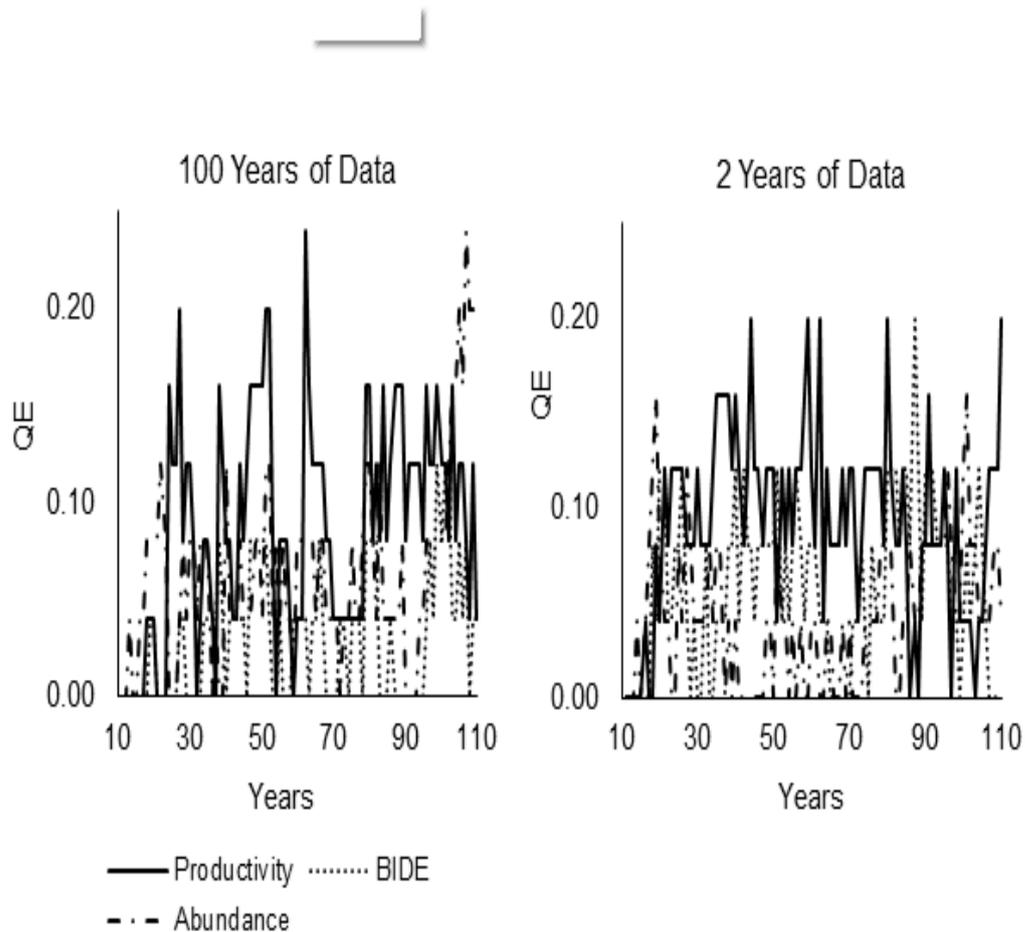


Fig. 5. Greater sage-grouse extinction responses to key source removals based on productivity, BIDE, and abundance-based source-sink metric prioritizations, calculated over 25 repetitions (graphs truncated to years 5-35). For a given year, higher probabilities of extinction (PE) indicated metrics with greater predictive value in identifying habitats with greater importance to regional population outcomes.

